

# Taxonomic Remarks on Cenozoic Pseudolivid Gastropods from South America

by

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*Abstract.* The neogastropod family Pseudoliviidae was represented in the Neogene of Peru and Chile by a single genus, which we name *Testallium* to replace *Gastridium* Sowerby, 1846, non *Gastridium* Sowerby, 1842, or *Gastridium* Modeer, 1793. Besides the type species, *Testallium cepa* (Sowerby, 1846), from the Miocene of Peru and Chile, we recognize *T. voluta* (Olsson, 1932) from the early Miocene of northern Peru, and *T. escalonia*, sp. nov. from the Pliocene of Chile. *Gastridium retusum* Philippi, 1887, is assigned to *Buccinorbis* Conrad, 1865.

## INTRODUCTION

The family Pseudoliviidae is a poorly known group of Late Cretaceous to Recent gastropod mollusks that, on the basis of shell characters as well as internal anatomy, belongs to the neogastropod superfamily Buccinoidea (see Cossmann, 1901; Squires, 1989; Kantor, 1991). Although the bathyal genus *Benthobia* Dall, 1889, is widely distributed in the Atlantic and southwestern Pacific Oceans, Recent shallow-water members of the Pseudoliviidae are restricted to subtropical and warm-temperate waters in western and southern Africa, the Australian region, and the west coast of North America. During the Miocene and Pliocene, however, the family was also represented on the west coast of South America by an extinct genus that has been referred to as *Gastridium* Sowerby, 1846. Unfortunately, *Gastridium* was preoccupied by *Gastridium* Sowerby, 1842, and Modeer, 1793. The distinctive South American Neogene pseudolivids therefore require a new generic name. In this paper, we (1) propose the genus *Testallium* for three Miocene and Pliocene pseudolivid species from Peru and Chile; (2) compare *Testallium* to other pseudolivid genera; (3) review the described species assigned or compared to *Gastridium* Sowerby, 1846, by previous authors; and (4) describe *Testallium escalonia*, sp. nov. from strata of probable Pliocene age in Chile.

Institutional abbreviations are as follows: BMNH, British Museum of Natural History, London, England; CAS, California Academy of Sciences, San Francisco, California, USA; PRI, Paleontological Research Institute, Ithaca, New York, USA; SGO PI, Museo Nacional de Chile, Instituto de Paleontología, Santiago, Chile; UCMP, Museum of Paleontology, University of California, Berkeley, California, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

## SYSTEMATIC PALEONTOLOGY

Class Gastropoda

Order Neogastropoda

Superfamily BUCCINOIDEA

Family PSEUDOLIVIDAE Cossmann, 1901

**Discussion:** Kantor (1991) has made cogent arguments for recognizing the Pseudoliviidae as a family distinct from such other families as the Buccinidae and Olividae with which it had previously been associated as a subfamily. In fact, anatomical peculiarities of the group prompted him to isolate the Pseudoliviidae in its own suborder Pseudolivoidei. This taxon was characterized by the presence of

a gland and valve of Leiblein, and by having the proboscis formed by the elongation of the buccal tube rather than by the elongation of the dorsal wall of the buccal cavity as in the suborder Muricoidei (Kantor, 1991). The most obvious shell character that distinguishes Pseudolividae from the Buccinidae (*sensu lato*) is the presence of a basal external spiral groove, which ends in a more or less prominent tooth or spine at the edge of the outer lip (Cossman, 1901). Other shell features that collectively set the Pseudolividae apart from other neogastropod groups include the following: notch or sinus at posterior end of outer lip; outer lip lying in a plane; spiral sculpture consisting of cords or threads that are strongest near base and weakest near upper part of whorl; aperture narrowly elongate; columella more or less concave on upper part, smooth; siphonal canal short to almost absent. Genera are distinguished on the presence or absence of apertural lirae (spiral riblets on the inner side of the outer lip), axial sculpture, an umbilicus, and a parietal rib, as well as on shell shape. A general review of the family by Vermeij is in progress.

#### Genus *Testallium* Vermeij & DeVries, gen. nov.

*Gastridium* Sowerby, 1846: p. 261; non *Gastridium* Sowerby, 1842: p. 312 (= *Pseudoliva* Swainson, 1840) (type species, *Buccinum plumbeum* Chem., = *Buccinum crassum* Gmelin, 1791); non *Gastridium* Modeer, 1793: p. 106 (type species: *Conus geographus* Linnaeus, 1758; Gastropoda: Toxoglossa: Conidae).

**Type species:** *Gastridium cepa* Sowerby, 1846 (pl. 1, figs. a, b)

**Diagnosis:** Pseudolid characterized by deep basal external groove terminating at outer lip in blunt labral spine; last whorl basally constricted above siphonal fasciole; fasciole adapically keeled; sculpture consisting of fine spiral threads over whole surface of shell above groove, and of two to eight strong spiral cords below groove; outer lip forming notch at adapical end of aperture; inner side of outer lip smooth; columellar callus of small extent; umbilical slit narrow or absent; parietal rib at adapical end of inner lip distinct.

**Etymology:** *testa* (Latin: shell) and *allium* (Latin: onion), referring to the specific name *cepa* (Latin: onion) of the type species.

**Discussion:** Sowerby (1842, p. 312) named the genus *Gastridium* to include *Buccinum plumbeum* Chem. (= *Buccinum crassum* Gmelin, 1791). In 1846 (p. 261), he introduced the name *Gastridium* again as a new genus, this time for *Gastridium cepa* Sowerby, 1846, a Miocene species collected by Charles Darwin in 1833 at Navidad on the central coast of Chile. In his 1846 paper, Sowerby (p. 261) noted that *G. cepa* was similar to *Buccinum plumbeum*, and that Swainson (1840, p. 82, p. 306) had made the latter species the type of *Pseudoliva* Swainson, 1840. Sowerby (1846) considered the name *Pseudoliva* "absurd" because *B. plumbeum* in his mind clearly belonged to the

"Buccini" rather than to the "Olivi." In fact, Sowerby assigned *B. plumbeum* to the buccinid genus *Eburna* Lamarck, 1822 (non Lamarck, 1801), whose oldest valid name is *Babylonia* Schlüter, 1838 (see van Regteren Altena & Gittenberger, 1981). Philippi also disliked the name *Pseudoliva*, and applied *Gastridium* Sowerby, 1846, to *G. cepa* and two other species, *G. opimum* (Hupé, 1854) and *G. retusum* (Philippi, 1887). The objective synonymy of *Gastridium* Sowerby, 1842, and *Pseudoliva* Swainson, 1840, was recognized by most subsequent authors, including Sowerby (1859), Cossman (1901), Melvill (1903), and Wenz (1938–1944). Moreover, the name *Gastridium*, as used by Sowerby (1842, 1846), was preoccupied by *Gastridium* Modeer, 1793 (p. 106), a well-known Indo-Pacific Recent member of the toxoglossan gastropod family Conidae. Gray's (1847, p. 136) introduction of *Gastridia* resolved the homonymy of *Gastridium*, but his name falls as an objective synonym of *Pseudoliva* because it was based on the same type species, *Buccinum plumbeum*. Sowerby (1846), Philippi (1887), and Olsson (1932) all regarded *Gastridium* in Sowerby's (1846) sense as distinct from *Pseudoliva*, but none of these authors offered distinguishing characters for the two groups. We agree that Sowerby's (1846) *Gastridium* refers to a distinct group, and propose the new genus *Testallium* for it.

*Testallium* differs from *Pseudoliva* in shape, sculpture, and the development of callus. Whereas *Testallium* is constricted (that is, distinctly concave in profile) just above the base of the siphonal canal, *Pseudoliva* is weakly convex to almost straight-sided. The fasciole of *Testallium* is prominent, marked by a keel-like posterior angulation. That of *Pseudoliva* is indistinct and rounded. *Testallium* has two to eight spiral cords below the basal groove, which conspicuously crenulate the edge of the outer lip; and numerous spiral threads between the groove and the suture. Earlier whorls carry fewer, somewhat stronger cords on the upper portion of the whorl. *Pseudoliva*'s shell, by contrast, is essentially smooth except for the basal groove. The columellar callus of *Testallium* is limited in extent, whereas that in *Pseudoliva* is broad, thick, and heavy, obscuring the basal groove on the ventral half of the last whorl.

Another similar genus is *Buccinorbis* Conrad, 1865, species of which are known from the late Paleocene (Thanetian) to the late Eocene (Priabonian). Like the Miocene to Recent West and South African *Pseudoliva*, it has extensive columellar callus, and the base is not constricted; but the groove is located relatively higher on the last whorl (see also Squires, 1989). Three to five strong spiral cords below the groove form well-defined crenulations on the edge of the outer lip below the labral spine (see also Palmer, 1937). *Buccinorbis* differs from *Testallium* by the absence of basal constriction, the large, heavy columellar callus, and the absence of a parietal rib at the adapical end of the inner lip.

The western North American early Miocene to Recent genus *Macron* H. & A. Adams, 1853, differs from *Testallium* chiefly by possessing lirae on the inner side of the



outer lip. The type species, *Buccinum aethiops* Reeve, 1847, is often extremely prominently sculptured with two heavy, rounded cords below the groove and up to six spiral cords above the groove. Other species, however, such as the early Miocene *M. hartmanni* Hertlein & Jordan, 1827 and the Pleistocene to Recent *M. lividus* A. Adams, 1855, and *M. orcutti* Dall, 1918, have fine spiral threads on the last whorl between the groove and the suture, and in this respect strongly resemble species of *Testallium*.

*Testallium* is strongly convergent on the Miocene to Recent western South American ocenebrine muricid genus *Chorus* Gray, 1847. Both genera have a broadly fusiform, basally constricted shell with a basal spiral groove ending in a labral spine at the edge of the outer lip. *Chorus* differs from *Testallium* by the absence of a posterior sinus in the outer lip, by lacking a parietal rib, and by having an indistinct, rounded siphonal fasciole rather than a markedly angulated one. The basal groove is also shallower and less conspicuous in *Chorus* than in *Testallium*. Moreover, *Chorus* has spiral sculpture consisting of six to seven widely separated primary spiral cords on the last whorl, which do not increase in prominence basally.

#### *Testallium cepa* (Sowerby, 1846)

(Figure 1a, b)

- Gastridium cepa* Sowerby, 1846, p. 261, pl. 4, figs. 68, 69.  
*Monoceros labiale* Hupé, 1854: pp. 199–200.  
*Monoceros opimum* Hupé, 1854, p. 200.  
*Fusus labialis* Hupé, 1854, pl. 3, fig. 3a.  
*Fusus opimus* Hupé, 1854, pl. 2, figs. 6, 6a.  
*Gastridium cepa* Sowerby, 1846: Philippi, 1887, pp. 59–60, pl. 6, fig. 2.  
*Monoceros labialis* Hupé, 1854: Philippi, 1887, pl. 5, fig. 1; not pl. 5, fig. 6 (indeterminate species).  
*Gastridium opimum* (Hupé, 1854): Philippi, 1887, p. 60, pl. 57, fig. 7.  
*Chorus* aff. *C. blainvillei* (d'Orbigny, 1842): Watters & Fleming, 1972: p. 398, pl. 28, fig. 6u; non *Chorus blainvillei* (d'Orbigny, 1842) (Muricidae).  
*Gastridium cepa* Sowerby, 1846: Tavera Jerez, 1979, p. 97, pl. 20, figs. 74, 75.

**Discussion:** *Testallium cepa* is a highly variable species, a fact that accounts for its long synonymy. The most variable character is the shoulder. The posterior (or anal) notch is strongly produced in the type specimen of *T. cepa*, and the shoulder is correspondingly well developed. Hupé's (1854) *Monoceros opimum* (labeled *Fusus* on his plate, and assigned to *Gastridium* by Philippi, 1887) represents an unshouldered shell in which the posterior notch is not produced. *Monoceros labiale* Hupé, 1854 (labeled *Fusus* on Hupé's plate, and assigned to *Monoceros* by Philippi, 1887) is intermediate between the *cepa* and *opimum* phenotypes. Philippi's (1887) illustration of *Gastridium opimum* (Hupé, 1854) (pl. 5, fig. 7) is indistinguishable from his illustration of *Monoceros labialis*.

Fleming (in Watters & Fleming, 1972) figured a poorly preserved specimen of *Testallium cepa* as *Chorus* aff. *C.*

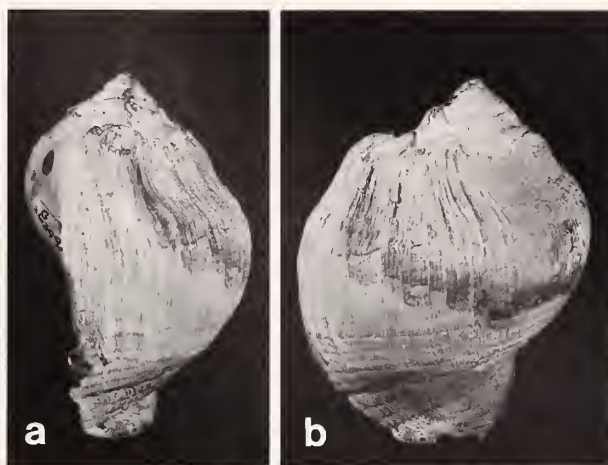


Figure 1

*Testallium cepa*. Holotype (BMNH G 26399); a, b. lateral and dorsal views. The shell is 5.5 cm in height.

*blainvillei* (d'Orbigny, 1842) from strata inferred to have been of early Pliocene age at Chepu, on Isla Chiloe, in southern Chile. They favored a Pliocene age in part because *Chorus* and several other genera in the fauna were not known from the Miocene at that time. The presence of distinctive Miocene fossils persuades us, however, that the Chepu beds are of late early Miocene age, and that they are correlated with the similarly aged strata of the Navidad Formation, from which *T. cepa* was originally collected (DeVries & Vermeij, in preparation). Fleming noted that the spiral sculpture of his specimen was weak, that the spire was higher, and that the shell was narrower than that of *Chorus blainvillei*. Moreover, his specimen lacked the nodes characteristic of *C. blainvillei*, a Pliocene species. Fleming's specimen represents a moderately shouldered form of *Testallium cepa*.

Two probably unrelated gastropods are strongly convergent in form, as well as in the expression and variability of the shoulder, to *Testallium cepa*. The Recent Panamic rapanine muricid *Vasula melones* (Duclos, 1832) often forms a keel-like ridge at the shoulder in its final stages of growth, whereas younger shells are weakly shouldered or rounded on the upper part of the last whorl. Every gradation between strongly shouldered and rounded shells can be found within populations throughout the range of the species. The "buccinid" *Triumphis distorta* (Wood, 1828), also from the Panamic Province, also shows a keeled, ridgelike shoulder in the adult stage and a rounded profile of the upper part of the body whorl in younger shells. It is striking that both *Vasula melones* and *Triumphis distorta* occur in rocky areas with intermixed sand, a habitat similar to that of the pseudolivids *Pseudoliva crassa* (Gmelin, 1791) and *Luzia zebrina* (A. Adams, 1855) in Angola (S. Gofas, personal communication to G. Vermeij, July, 1995).

*Testallium* occupied a similar habitat in Peru and Chile. In Chile, *T. cepa* is found in pebbly sandstones of probable

early Miocene age (DeVries & Vermeij, in preparation) near basement rocks at Punta Ahuenco on the east coast of Chiloe (Watters & Fleming, 1972); in massive sandstones at Islas Ipun and Stokes, south of Chiloe (DeVries et al., 1984); and in fine to medium-grained sandstone in the Navidad basin (Tavera Jerez, 1979), sometimes in strata with intercalations and lenses of gravel. In the Pisco Basin of southern Peru, specimens of *Testallium* are found in coarse-grained sandstones at numerous localities. At Callejon de Cerro de Piedra, near Nazca (Rivera, 1957), specimens of *T. cepa* occur with numerous specimens of *Turritella woodsii* Lisson, 1925, in probably early Miocene conglomerates and coarse-grained sandstones directly overlying basement crystalline rocks. In the Lomas Chilcatay, east of Bahía de la Independencia, specimens of *T. cepa* are found together with a diverse assemblage of early early Miocene mollusks in basal sandstones of the Chilcatay Formation and in bioclastic, balanid-rich sandstones higher in the same section that have been dated as late early Miocene (Dunbar et al., 1990).

**Distribution:** Early Miocene (*Rocella gelida* Zone to *Triceratium pileus* Zone, about 24–18 Ma; H. Schrader, written communication, 1987), southern Peru to southern Chile.

*Testallium voluta* (Olsson, 1932)

*Acanthiza* (*Chorus*) *voluta* Olsson, 1932: pp. 184–185, pl. 19, figs. 3, 6, 7.

**Discussion:** *Acanthiza* Fischer is probably a misspelling of *Acanthina* Fischer de Waldheim, 1807, another genus with a labral spine from western South America. *Chorus* Gray, 1847, is yet another genus with a labral spine from the same region. Olsson (1932) compares *T. voluta* with *Monoceros laevis* Philippi, 1887 (= *Chorus laevis*). Specimens of *T. voluta* are distinguished from those of both *Acanthina* and *Chorus* by their strong axial folds on the earliest whorls and anal notch.

Differences between *T. voluta* and *T. cepa* are more subtle. Specimens of both species show strong spiral cords on the earliest whorls, but only *T. voluta* shows any axial sculpture. What most distinguish specimens of *T. voluta* are a short siphonal canal (well under half the apertural length) and, in adult specimens, a weak to moderate sulcus on the body whorl that lies anterior to a moderately angulate, tabulate shoulder. Shouldered specimens of *T. cepa*, in contrast, have sloping shoulders, no sulci so low on the body whorls, and moderately produced siphonal canals (equal to half the apertural length).

*T. voluta* was considered by Olsson (1932) to be ancestral to *Clavella solida* Nelson, 1870, from the late Miocene Cardalitos Beds of northern Peru (Olsson's 1932 figure of *T. voluta* is excellent, and the reader is referred to it for illustration). Olsson (1932) assigned Nelson's species to what he called *Acanthiza* (*Chorus*). Our examination of type material of *Clavella solida* (Yale Peabody Museum YPM 00507) reveals that *C. solida* has strong axial ribs on early teleoconch whorls, as does *Testallium voluta*, but it lacks the basal groove of *T. voluta* and other species of

*Testallium*. Apertural features are obscured by matrix. Nelson (1870, p. 199) suggested that *Clavella solida* is related to *Triumphis distorta* (Wood, 1828). We tentatively assign it to the genus *Nicema* Woodring, 1964, which is usually included with *Triumphis* Gray, 1857, in the family Buccinidae (see Woodring, 1964).

Specimens of *T. voluta* from northern Peru are filled with a coarse-grained bioclastic matrix. Olsson (1932) proposed with some uncertainty that they were collected at the base of shales from the Heath Formation, overlying Punta Bravo "grits." Olsson (1932) believed the Heath Formation to be of Oligocene age, but subsequent work by Zuñiga & Cruzado (1979) indicates its age to be early Miocene.

*Testallium escalonia* Vermeij & DeVries, sp. nov.

(Figure 2a, b)

**Diagnosis:** *Testallium* with a relatively high spire (spire one-fourth to one-third shell height), 17 to 23 fine spiral threads on last whorl, and narrow umbilical slit.

**Description:** Shell relatively high-spired, consisting of five teleoconch whorls separated by shallow, appressed sutures; spire one-fourth to one-third total shell height; sculpture consisting of two cords below basal groove, and 17 to 23 fine spiral threads between the groove and the suture on the last whorl, increasing in strength toward the base; last quarter of body whorl marked with closely spaced growth lines; groove terminates in small blunt labral tooth at edge of outer lip; fasciole prominent, sharply angled posteriorly, rounded below; narrow umbilical slit on inner side, edge faintly crenulated in accordance with external spiral sculpture; columella bearing five or six low oblique ridges on lower half; weak anal notch where outer lip joins penultimate whorl posteriorly.

**Holotype:** CAS 66806.01, height 34.0 mm, diameter 24.2 mm, aperture height 25.4 mm.

**Paratype 1:** CAS 66806.02, height, 28.9 mm, diameter 19.7 mm, aperture height 21.4 mm.

**Paratype 2:** UCMP 39880, height 25.4 mm, diameter 15.8 mm, aperture height 20.5 mm.

**Type locality:** El Ganso (*ganso* = goose), 34°13'S, west of Fundo Las Damas, also known as the La Cueva Locality. La Cueva Formation of probable late Pliocene age, Chile.

**Etymology:** Latin noun for small onion.

**Discussion:** *Testallium escalonia* differs from the older *T. cepa* chiefly in having a higher spire (spire one-fourth to one-third as compared to one-seventh of shell height as in *T. cepa*) and in being less constricted at the base of the siphonal canal, which is relatively shorter. Herm (1969) did not record this or any other species of *Gastroidium* (our *Testallium*) from the Pliocene of Chile. Oddly enough, the holotype and Paratype 1 were collected by Herm. He



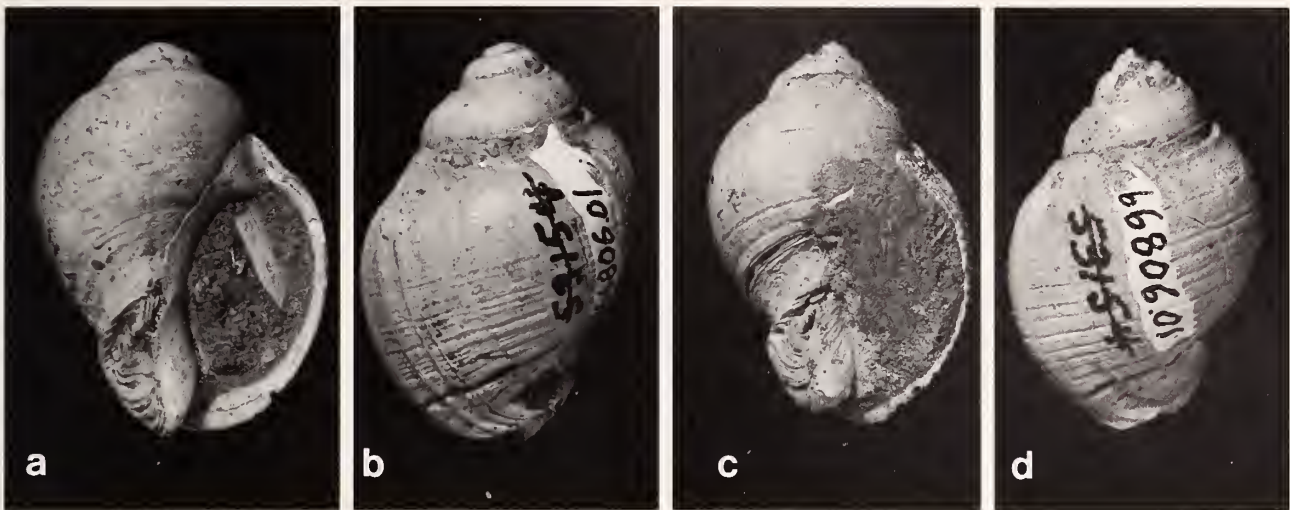


Figure 2

*Testallium escalonia*. Vermeij & De Vries, sp. nov. a, b, holotype (CAS 66806.01), ventral and dorsal views; c, d, paratype 1 (CAS 66806.02), ventral and dorsal views. The holotype (a, b) is 4 cm in height; the paratype (c, d) is 3.5 cm in height.

may have mistaken them for worn specimens of the muricid genus *Chorus*, which superficially resembles species of *Testallium*.

The precise age of the La Cueva fauna is not entirely clear, but it appears to be Pliocene (Herm, 1969).

*Testallium escalonia* is the youngest known species of its genus. Along with many other genera and species, *Testallium* evidently became extinct near the end of the Pliocene in western South America.

#### Genus *Buccinorbis* Conrad, 1865

Type species. *Buccinum vetustum*, Conrad, 1833

#### *Buccinorbis retusa* (Philippi, 1887)

*Gastridium retusum* Philippi, 1887. p. 59, pl. 6, fig. 3, 3b.

*Pseudoliva parinasensis* Woods, 1922, p. 93–94, pl 12, figs. 4–6.

*Pseudoliva parinasensis* Woods: Olsson, 1928, p. 123.

**Discussion:** Philippi (1887) recognized three species of *Gastridium*: *G. cepa* Sowerby, *G. opimum* (Hupé), and *G. retusum*, Philippi, 1887. Of these, the first two are referable to a single species of *Testallium* (see above), but *G. retusum* is distinct. A cast of Philippi's holotype (SGO PI 765), as well as Philippi's figures, shows that the species belongs to *Buccinorbis* Conrad, 1865. Like other species of *Buccinorbis*, *B. retusa* has the spiral groove at a relatively high position on the last whorl, and lacks basal constriction. There is a strongly developed columellar and parietal callus. None of the known specimens has the aperture exposed or the outer lip intact. Philippi (1887) thought *B. retusa* to be of Cretaceous age, but strata at the type locality (Algarrobo, Chile) are Eocene (Tavera Jerez, 1979).

Judging from the figures, *Pseudoliva parinasensis* Woods,

1922, from the early Eocene of northern Peru, is a subjective synonym of *B. retusa*. We have been unable to locate Woods's holotype to confirm this suspicion. According to Olsson (1928), *B. parinasensis* occurs in the Salina, Negritos, and Parinas Formations of early to middle Eocene age. The extent of callus formation is variable in this species, as is the strength and extent of spiral sculpture on the last whorl between the spiral groove and the suture. The specimen described from the middle Eocene of Colombia as *Pseudoliva (Buccinorbis)* cf. *P. (B.) parinasensis* by Clark & Durham (1946) differs from *B. retusum* and Woods's *P. parinasensis* from Peru by possessing an umbilicus. This feature may well have been variable in *B. retusa*, but we prefer to keep Clark & Durham's (1946) Colombian *parinasensis* form outside the limits of *B. retusa*.

Olsson's (1928) variety *samanica* from the late Eocene Talara and Saman beds (=Verdun Formation) of northern Peru is more heavily callused, larger, and less rotund than is *B. retusa*, and has a narrower anterior end. Forms questionably assigned to this variety were described from the late Eocene of Colombia (Clark & Durham, 1946) and Curaçao (Jung, 1974). Olsson's (1928) variety *mancorensis* has a laterally flattened rather than an evenly rounded last whorl and a massive callus in the columellar and parietal regions of the shell. The final stages of growth are characterized by adapical migration of the outer lip and by the increasing prominence of the shoulder. This variety was described from the Chira, Mancorá, and Heath Formations, all regarded as Oligocene by Olsson (1928). The Mancorá and Chira Formations, however, are of latest Eocene age (Zuñiga & Cruzado, 1979), and the occurrence of the *mancorensis* form in the Heath Formation, which is early Miocene, is questionable. We tentatively retain the varieties *samanica* and *mancorensis* of Olsson, 1928, as

stratigraphic subspecies of *B. retusa*, but further work and additional material may reveal that all are members of a single, long-ranging species in which whorl profile, callus development, late-stage shouldering, expression of spiral sculpture, and size are all highly variable traits. *Pseudoliva* (*Buccinorbis*) *vientoensis* Clark & Durham, 1946, from the Eocene of Colombia, may also prove to part of this variation.

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